Habitat use by roe deer (*Capreolus capreolus*) under the predation risk of lynx (*Lynx lynx*) and humans: A life in the squeeze between two contrasting predators

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Preface

This scientific work was conducted at the University of Oslo, Norway, from the summer 2012 to spring 2014 under the supervision of Atle Mysterud, Leif Egil Loe and Karen Lone. To make a long story short, since I was a boy, in Skogbygda, stories about the scientific work of Atle Mysterud has inspired me to take step by step to reach that day I could be one of his students. I actually reached that goal! I would like to thank Atle for exceptional supervision and many good talks, especially those about roe deer hunting in Skogbygda. In addition, I would like to thank Leif Egil Loe for guidance in R and thereof logistic regression. Karen Lone deserves a special thank, I could never been more lucky to have a more confident PhD student in cooperation during the field work. Rune Sørås deserves thanks for his contribution as field assistant. I would also like to thank hunters in Buskerud, Vestfold and Telemark which showed me their roe deer kill sites. Without them, a part of this study could never been done. Thanks go to John Odden and John Linnell for sharing data from the Scandlynx project.

I have also to thank people at room 4317 for many cheerful conversations. Further thanks go to people at room 3320, especially Anne Marie Dalen and June Susanne Berg, for support during the bachelor and master. Kristine Dalen, Marie Sørum and Trude Kristiansen also deserves several thanks, I appreciate your smiling faces when I "forage" at Blindern. I also thank Ingunn Solbakken for proofreading.

Many thanks go to my mother Hilde Kvernhaugen Norum and my brothers, Emil, Peder and Jakob. Inspiration to conduct this thesis was found during several hours with physical activity, bush walking, grouse leks, fishing and hunting trips with friends. At last, a thank goes to my father Arild Norum that showed me the way in to the wilderness where the biology exists.

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Abstract

Predator efficiency may depend on habitat characteristics that vary in the physical landscape, and there may thus be a spatially heterogeneous distribution of predation risk. Prey might alter habitat use or change behavior as a predator avoidance strategy to reduce the direct lethal effect of predation. In this way, indirect effects of predation may happen if prey by their habitat use is trading off resource availability against reduced predation risk. In presence of one predator, a fitness enhancing anti-predator response might be easily singled out since prey can use habitats where the hunting success of this predator is low. However, prey may be exposed to multiple predators that show different patterns of spatial hunting success due to their hunting styles. Hence, how habitat use by ungulates is influenced by the risk of being killed by natural predators and humans has become topical in light of the re-colonization of apex predators and extensive human harvesting. My main aim with this study was to determine how risk habitats of roe deer (*Capreolus capreolus*) were under the predation risk of lynx (*Lynx lynx*) and humans in southeastern Norway. Differences in habitat characteristics between kill sites and random sites used by roe deer were used as a proxy of predation risk. The spatial predictability of hunters was investigated by comparing habitat characteristics at kill sites where different weapon types and hunting methods had been used. I predicted that the risk of lynx predation was high in dense habitats, while open habits gave higher risk of being shot. I also predicted that the risk of being shot by a hunter was dependent on hunting method and the use of rifle and shotgun. The risk of being killed by lynx was related to dense habitats, while hunters imposed in general greater risk in open habitats. Habitat use by roe deer was squeezed between the risk habitats of these contrasting predators. Comparison of vegetation density between kill sites where different weapon types and hunting methods had been used indicated that the hunter is flexible and impose risk across the environmental range of habitat characteristics. In a broad perspective, roe deer cannot avoid the risk imposed by these predators by using one single spatial predator avoidance strategy. Due to a relatively flat overall risk landscape, the behavior of roe deer seems to be to avoid starvation and face the direct lethal effect of predation.

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1. Introduction

Until recently, mainly the direct lethal impact of predation has been considered. However, prey populations do not only suffer through direct lethal effects (Valeix et al. 2009). Presence of a predator might also affect resource availability, foraging decisions, vigilance and stress levels (Sih 1980, Werner et al. 1983, Brown et al. 1988, Lima and Dill 1990, Krebs et al. 1995). The ecology of fear has expanded this view by putting the indirect aspects of predation into a more coherent framework than previously, giving higher understanding of the distribution of prey and predator (Brown et al. 1999, Laundre 2010). Predation risk creates a mosaic of risky habitats and refugees in the physical landscape since the efficiency of a predator vary among habitat characteristics (Kauffman et al. 2007). The distribution of risk can thus be illustrated as a landscape with risky peaks and safe valley bottoms, termed the "landscape of fear" (Laundré et al. 2010). A heterogeneous spatial distribution between prey and predator are likely to occur because of prey concentrating their activity in low risk areas (Sih 2005, Laundre 2010). Habitat use, behavior, and time allocation that reduce the risk of predation can then be viewed as an adaptive predator avoidance strategy (Laundre et al. 2001). The cost of using safe habitats can thus provide indirect effects of predation since the availability of resources are often traded off against reduced predation risk (Brown 1992, Brown 1999).

As an example of indirect effects, Fortin et al. (2003) investigated the interaction between elk (*Cervus elaphus*) and wolves (*Canis lupus*) in Yellowstone National Park, USA. They concluded that elk selected less forage-rich winter habitat after wolf re-colonization than they had done before. The wolves forced elk into denser habitats which secondarily led to reduced browsing pressure in the preferred open habitats, making changes in the vegetation community (Creel et al. 2005). As a result, by changing their habitat use as an anti-predator response to the presence of wolves, elk had reduced overall survival, growth and reproduction in their new habitat (Christianson and Creel 2010). Reduced reproduction, linked to changes in reproduction physiology, is one consequence of the indirect effects of predation due to the change in food availability (Creel et al. 2007). Several studies have thus suggested that reintroduction of wolves induce a behavior mediated trophic cascading effect that has important repercussion for the whole ecosystem dynamics in Yellowstone (Ripple and Beschta 2003, Ripple and Beschta 2004, Fortin et al. 2005, Mao et al. 2005, Ripple and Beschta 2006, White et al. 2008, Ripple and Beschta 2012). Nevertheless, these issues are still heavily debated and further research is required before we fully understand the importance of indirect effects and their consequences (Kauffman et al. 2010, White et al. 2011, Beschta and

Ripple 2013, Boonstra 2013, Kauffman et al. 2013, Middleton et al. 2013).

A predator avoidance strategy may become even more complex if prey have to respond to interactions with multiple predators at the same time in the same space (Sih et al. 1998). Predation risk by more than one predator has rarely been considered in the analyses of risk connected to habitat selection by ungulates (Theuerkauf and Rouys 2008, Atwood et al. 2009). Although humans serve a role as predator alongside large carnivores in many ecosystems, few studies include the hunter as a predator (Theuerkauf and Rouys 2008, Proffitt et al. 2009, Lone et al. 2014) despite that hunting risk possibly influencing the spatial distribution of ungulates (Proffitt et al. 2013). How ungulates perceive and respond to predation risk by natural predators and hunters in the same ecological space is thus not well understood.

In Norway, the roe deer (*Capreolus capreolus*) is living in a landscape with a mix of farmland and forest where the habitat use is related to the availability of cover and forage (Selås et al. 1991, Mysterud et al. 1999, Herfindal et al. 2012). Roe deer are hunted by lynx (*Lynx lynx*) as well as hunters (Odden 2006, Andersen et al. 2007). How roe deer respond to hunters as a predator have rarely been investigated (Benhaiem et al. 2008). Hunters are most efficient in open terrain because they use rifles and can shoot from long distances (Farmer et al. 2006, Ciuti et al. 2012). In contrast, big felids such as the lynx are stalking predators dependent on cover for successful ambush attacks (Dunker 1988, Nilsen et al. 2009, Laundre 2010). Because of different hunting styles, the contrasting predation risk imposed by lynx and hunters are likely to influence how roe deer allocate the time among habitats (Benhaiem et al. 2008). A heterogeneous spatial distribution between roe deer and these predators might then exist.

In this study, I investigate the indirect part of the interaction between roe deer and its two main predators, namely the lynx and hunters. I am going to identify characteristics of risky habitats for roe deer, where hunters and lynx are expected to impose a contrasting risk in the physical landscape. Differences in habitat characteristics between kill sites and random sites used by Global Positioning System (GPS) marked roe deer will be used as a proxy for how predation risk is distributed. Although wolf kill sites are criticized for having low relevance to determine predation risk (Beschta and Ripple 2013), the hunting styles and immediate outcome of an encounter with lynx and hunters should mean that kill sites are found in the risk habitats (Schmitz 2008). Specifically, I will test the hypotheses that vegetation density modulates predation risk due to the hunting styles of humans and lynx. Hence, I predict that vegetation density will be higher at lynx kill sites than at random roe

deer sites, and lower at hunter kill sites than at random roe deer sites. I will in addition evaluate whether roe deer make tradeoffs between safe and risky areas, and whether this might impose indirect effects of predation due to reduced resource availability. I also extend recent related studies on this topic (Lone et al. 2014) by considering how risk by hunters may vary depending on hunting methods and the use of rifle and shotgun. An overview of hypotheses and corresponding predictions are given in table 1.

Table 1: Overview of hypotheses and predictions for how roe deer face risk of being killed by lynx and hunters.

Hypotheses and predictions	
H1.	**The risk of lynx predation is high in dense habitats due to better stalking conditions, and roe deer may face a tradeoff between availability of cover and risk of being killed.**
H1.1	Roe deer are exposed of being killed by lynx in habitats with increasing vegetation density and decreasing visibility.
H1.2	Lynx kill sites have low quantity of forage, for example herbs, grass, ericaceous species and RAG (rowan, aspen and goat willow).
H2.	**The risk of being shot by hunters is high in open habitats due to higher opportunity of detecting a roe deer and initiate clean shots, and roe deer may face a tradeoff between the forage availability and the risk of being shot.**
H2.1	Roe deer are exposed of being shot by hunters in habitats with decreasing vegetation density and increasing visibility.
H2.2	Hunter kill sites have higher quantity of good forage, like herbs, than random sites used by roe deer
H2.3	The vegetation density is denser where roe deer are shot by shotgun compared to rifle.
H2.4	The vegetation density is more open for waiting hunters using more open habitats to detect the roe deer than hunters stalking it or using drive hunting.
H2.5	Roe deer adaptively move in to denser habitats to reduce its risk of being shot during the hunting season.

2. Material and methods

2.1 Study area

The fieldwork took place in the counties Buskerud, Vestfold and Telemark in southeastern Norway from 20th of June to the 22nd of July 2012 (9°45'E, 59°20'N, Fig. 1). Most of the visited sites were in the forest of the Fritzøe estate. The study area was located within the boreonemoral and southern boreal zone (Abrahamsen et al. 1977). The forest was dominated by Norway spruce (*Picea abies*), Scots pine (*Pinus sylvestris*), and European white birch (*Betula pubescens*), but rowan (*Sorbus aucuparia*), aspen (*Populus tremula*) and goat willow (*Salix caprea*) occurred at some places. Grey alder (*Alnus incana*) and black alder (*Alnus glutinosa*) were present along rivers and bogs. European ash (*Fraxinus excelsior*), common hazel (*Corylus avellana*), little leaf linden (*Tilia cordata*) occurred at sunny locations, and even elm (*Ulmus glabra*) was present at some sites. The shrub layer was dominated by ericaceous species like bilberry (*Vaccinium myrtilus*) and heather (*Calluna vulgaris*). Different species of herbs, like common cow-wheat (*Melampyrum pratense*), grass species such as crinkled hairgrass (*Avenella flexuosa*) and mosses were common in the field layer. Infield pastures consisted mainly of meadows and crop land located on fertile ground near the major river Numedalslågen in Buskerud and Vestfold, while they were more scattered distributed on flat areas in Telemark. The topography in Buskerud and Vestfold was characterized by gently slope areas near the Numedalslågen with steep hills dominating above. The same type of topography existed in Telemark, but the hills were much steeper.

This area has hosted a large roe deer population in the 1990`s, but after the lynx population started to increase in the middle of the 1990`s, local hunters have experienced a gradual reduction in the population (conversations with local hunters). An estimated number of ca 500 roe deer is killed by lynx in the study area every year, but the number vary from approximately 250 – 900 individuals (pers. comm. J. Odden). Roe deer`s risk of being killed by lynx will likely be influenced through the management/harvest of the lynx population. Considering the lynx management, the study area is located inside the management unit "rovviltregion 2". This region consists of the counties Buskerud, Vestfold and Telemark in addition to Aust–Agder. The politically determined population size for this region is 12 family groups, where one family group is comprised of one female lynx and her cubs (Hanssen 2012). The county governor and "rovviltnemnda" are responsible for the management, and a yearly hunting quota is given if the population reaches the agreed density. Approximately 30 lynx, thereof almost 10 females, are legal game from the 1st of February to

the 30th of March every year, but the quota varies due to uncertainty in population size (Rovviltnemda 2013, Rovviltnemda 2014). The annually outtake is usually reached since lynx hunters are effective (Brainerd et al. 2005), but the number of shot individuals are dependent on the outtake of adult females.

On average 320 roe deer are harvested by hunters in Buskerud and Telemark every year, while the number is 840 for Vestfold (Naturdata 2013). Adult males are legal game from 10th of August to the 24th of September, and rifle is the only legal type of weapon in this time of the season. From the 25th of September to 23th of December, all individuals are legal game and hunters can use rifle and shotgun as well as small dogs. In the early period when only adult males are hunted, the main methods used are the "sit and wait" and the stalking method. Drive hunting with and without small barking dogs is more common to use in the late period.

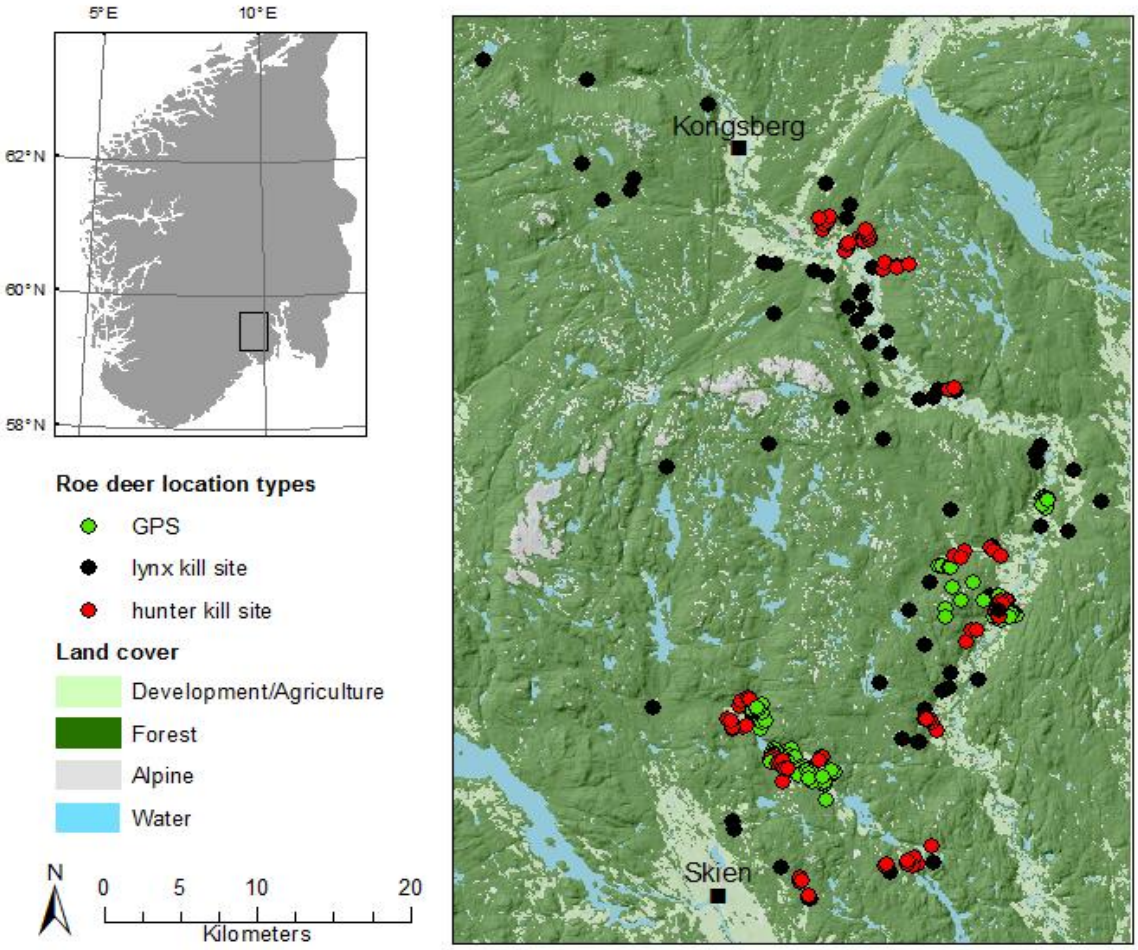

Figure 1: Map of the study area that compromises parts of the Buskerud, Vestfold and Telemark county, Norway, showing random GPS sites from roe deer (n=120), lynx kill sites (n=68) and hunter kill sites (n=102). Land cover types are included.

2.2 Study design - random sites used by roe deer and kill sites

The basis for this study was a dataset consisting of habitat characteristic measurements from 68 sites where roe deer were killed by lynx, 120 random sites derived from ten GPS-marked roe deer (88 sites from females and 32 sites from males) and 102 sites where roe deer were shot by a hunter.

Sites where roe deer had been killed by lynx derived from the Scandlynx project. All these sites had been verified and localized by several field inspectors by identify clusters of positions from GPS-marked lynx in the time period 2008 – 2012 (Scandlynx 2013). Thereof, all sites originated from nine different lynx, four females (F220, F229, F252 and F290) and five males (M250, M251, M255, M271 and M294).

Random roe deer GPS sites was collected from ten individuals in a collaborative project between NINA (The Norwegian Institute for Nature Research), UoO (University of Oslo) and NMBU (Norwegian University of Life Sciences). A random sub-sample of all the available roe deer sites was chosen by using a stratified selection of sites from all individuals given three season categories. The seasons were defined as summer (1 May – 9 August), hunting season (10 August – 23 December) and winter (24 December – 31 April). Since data from the hunting season was missing for five of the ten individuals, data related to the hunting season was only derived from the five remaining individuals to ensure a uniformed distribution of sites between seasons (Table 2).

All coordinates for lynx kill sites and random roe deer sites were downloaded to a handheld GPS unit from Garmin by using MapSource 6.16.3. This handheld GPS was used to reach all the sites in the field. The GPS positions for both lynx kill sites and random roe deer sites had an uncertainty of 5 – 10 meters compared to the true position due to the handheld GPS itself. Therefore, to have the same reference point and the same type of uncertainty at both lynx kill sites and random roe deer sites, I consistently used the first "zero point" on the handheld GPS as the determination of the sites. This was also done despite bone findings nearby the "zero point" at lynx kill sites.

Table 2: Random roe deer sites were collected from ten roe deer. A subset of sites was used of all available sites. Note that the positions during the hunt were missing for some individuals.

	Individuals										
Season	R0003	R0006	R0007	R3069	R3070	R3071	R3072	R3073	R3074	R3075	Sum
Hunt	8	0	0	8	0	0	0	8	8	8	40
Summer	4	4	4	4	4	4	4	4	4	4	40
Winter	4	4	4	4	4	4	4	4	4	4	40

Hunter kill sites were shown by 15 local recreational hunters. A hunter kill site was defined as the position of the deer when the hunter fired the first shot. All coordinates were marked on the handheld GPS, and the "zero point" was determined as the position shown by the hunter. In most cases, the hunter knew exactly where the shot had been initiated, which then became the position. In a few cases, the hunter did not exactly remember the site. In these cases, I established the site at a position where the hunter thought it was likely that the deer had been standing. This happened at 11 of the 102 hunting kill sites, and I find this unlikely to have biased my results. Type of weapon used during the hunt and the hunting method was noted where the hunter remembered this type of information. Weapon types were classified to be either shotgun (n=23) or rifle (n=69). If a combination weapon was used, type of weapon for the shot was noted. Hunting methods were divided in three categories comprising of drive hunting (n=62), "sit and wait" (n=22) and stalking (n=15). This information was collected to examine the predictability of the predation risk imposed by hunters. Information on sex and age for the shot deer was also registered.

Considering all hunter kill sites, I used no sites older than five years (2007 – 2012). This was done to avoid differences in habitat characteristic due to succession processes from the actual habitat characteristics when roe deer were shot. In addition, this was favorable since all lynx kill sites and random sites used by roe deer were related to the same time period.

2.3 Habitat characteristic measurements

Habitat characteristics were measured inside a circle of 50 m in radius with the GPS – coordinates, the "zero point", as the center of the circle (Fig. 2). The circle was divided in four different sectors with north, east, south and west as the orientation. All measures were taken from the "zero point" in every orientation. This gave four measures of the habitat characteristics at each site. A mean of these measurements were calculated and used in the analyses.

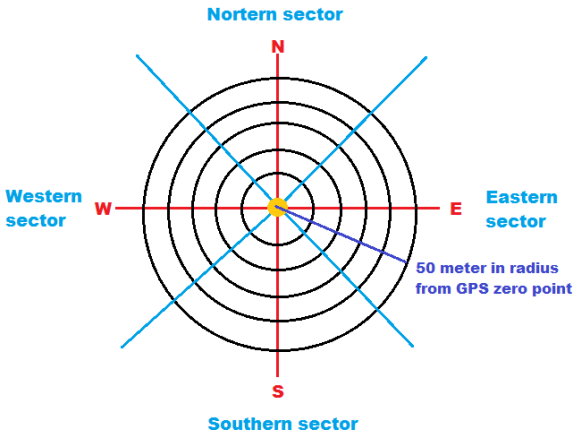

Figure 2: Illustration of the orientation at a site in the field. Habitat characteristics measurements were measured in northern, eastern, southern and western sector, with north (N), east (E), south (S) and west (W) as the orientation in every sector. All habitat characteristics measurements were taken from the "zero point" in center of the circle with 50 m radius. The circles represent the separation of each tenth meter up to 50 m.

Tree basal area: A measure of tree basal area (m^2 /ha) was registered by using a chain-relascope (Fitje 1996). The tree basal area is defined as a section of land that is filled by tree trunks (Hedl et al. 2009). Measurements were collected by putting the end of the chain relascope down under the aiming eye and look through the factor opening when the chain was completely extended. Trees that filled the factor opening in the relascope were counted and separated in different categories comprising of Norway spruce, Scots pine, European white birch, RAG (rowan, aspen and goat willow) and others. The relascope facor depends on the length of the chain and factor opening. A relascope with factor 1 has a chain length of 50 cm and a factor opening of 1 cm. When using factor 1, the trees counted are proportional to the basal area in (m^2 /ha). I also used relacope factor 0.5. The number of trees counted were in these cases multiplied with the relascope factor to get the real estimate of basal area (m^2 /ha) occupied by the categories.

Visibility and concealment: The visibility of a roe deer was measured by counting the number of open squares in a cover board (Griffith and Youtie 1988, Mysterud and Østbye 1999). The cover board was separated in four gridded sectors called L1 (body lying), L2 (head lying), H1 (body upright) and H2 (head upright), where every sector had 20 squares that were 5 cm in height, and 6 cm in width. In full size, the cover board was 80 cm high and 30 cm wide. Visible squares were counted at 10, 20, 30, 40 and 50 m from the cover board. The distance to concealment was also registered. All measurements took place in knee-standing position to mimic how the lynx perceive the horizontal vegetation cover. A lot of hunters are sitting on the ground or their backpack when they are hunting, thus this sampling method is likely to represent a fair estimate of visibility for both predators.

Canopy cover: Canopy cover was measured by using a spherical densiometer model C (Lemmon 1956). The densiometer gives an estimate of canopy cover by counting covered squares in a gridded mirror (Yocom and Bower 1975). The densiometer contains 24 squares, where each square is divided in 4 sub-squares. Canopy cover is thus expressed as the fraction of 96 small squares that are covered (Fig 3). By multiply the number of covered squares by 1.04, a percentage estimate of canopy cover is given. In field, canopy cover was measured by holding the densiometer in chest height level, approximately 1.3 m above ground level, and then counting the squares. If one branch hung out and covered the whole densiometer, one step aside was taken to get an estimate of the canopy cover instead of "branch cover".

Figure 3: Canopy cover was measured by using a concave spherical densiometer. This type of densiometer consists of 24 squares, where each square is divided in 4 smaller squares. I registered canopy cover by counting covered squares.

Proportion of potential forage: In a 2 m x 2 m square centered on the "zero point", I estimated percentage cover of functional plant groups to evaluate the relative availability of forage. These groups were 1) dead material, 2) grass, 3) herbs, 4) ericaceous species, 5) ferns and horsetails and 6) mosses. In addition, inside the same square, I counted the number of RAG stem recruits with foliage below 1.5 m above the ground level.

2.4 Statistical analyses

Statistical analyses were conducted in R version 2.13.1 (R Core Development Team 2011). Note that the sampling period was the same for all sites irrespective of year and season of the original position. In the following analyses, I assumed that habitat characteristics were fairly stable through the short time frame they were sampled.

2.4.1 Mean calculations and transformations

In order to obtain homoscedasticity, the data material was treated in different ways to fit the normal distribution. The mean canopy cover and the proportion of forage was transformed with arcsin[sqrt(percentage canopy cover or proportion of forage /100)] since they were measured as percentages. RAG measures were ln+ 1 transformed. A mean of tree basal area in (m^2/ha) for each category was calculated and transformed with ln+1. Considering the visibility measurements from the cover board, the mean visibility of a roe deer was computed. This was done by summing the number of open squares in the cover board for all sectors, (L1, L2, H1 and H2) at all distances and dividing on the units composed. The mean shortest distance to concealment for a deer was also computed by summing the distances where the cover board disappeared for each orientation and divided on four. Both the mean measure of a deer and the mean distance to concealment were transformed with ln+1. Diagnostic plots were used to investigate the normality, constancy and how single observations influenced the data. The "polycor" package in R with the "hetcor" function was used to determine the correlation between numerical variables (Fox 2010). This was done for the untransformed mean measurements for all habitat characteristics.

2.4.2 Quantification of differences between kill sites and random roe deer sites

My predictions were investigated by comparing differences in habitat characteristics between kill sites and random sites used by roe deer, using Generalized Linear Models (GLM). Transformed variables of canopy cover, tree basal area, distance to concealment and proportion of potential forage were used as response variables while type of sites, sex and seasons as the explanatory variables. I selected to use only basal area of spruce and pine as the tree categories. The proportion of grass, herbs, ericaceous species and RAG were selected as

the forage variables. My main argument to only include these variables is due to their biological relevance for investigating my predictions. Since the hunting season is one type of season, these data was removed when differences between seasons was compared. Canopy cover was used as the only response variable to investigate whether it was differences at lynx kill sites and random roe deer sites among season. A forward model selection approach was done using the Akaike Information Criterion (AIC) (Burnham and Anderson 2002). Interactions between the chosen variables were included in my analyses. According to the principle of parsimony, I chose the model with lowest AIC value since this gives the best balance between variation explained and number of parameters included. The simplest model was chosen if models $\Delta AIC < 2$. Overdispersion was avoided by checking that residual deviance was lower than the residual degrees of freedom.

For a subset of data, the same statistical approach with the same response variables but with weapon types and hunting methods included as explanatory variables was used to investigate the variation among hunter kill sites. Separate models were made for weapon types and hunting methods since shotguns were only used during drive hunting.

For plotting, models without transformed variables were used since this intuitively is more illustrative for the reader. Numbers in the result text are back transformed estimates given as mean and 95 % confidence interval.

2.4.3 Differences among roe deer and lynx individuals

Generalized Linear Mixed Models (GLMM) were used to search for potential influence due to distinctive differences among individuals of roe deer and lynx. For both roe deer and lynx, a GLMM with the individual identity as the random factor was compared with the GLM. AIC values were used to determine which of the models that had the best performance.

2.4.4 Examination of predation risk along vegetation density gradients

The previous analysis aimed to determine characteristics at the average location. To estimate how the predation risk varied across continuous vegetation density gradients, investigating prediction H1.1 and H2.1 deeper, the relative probability of being killed was estimated by using GLM but with a logistic regression approach (i.e. assuming a binomial error term). Separate models were made for the relative risk of being killed by lynx and hunters. A binary response variable was created for lynx and hunter kill sites (both with response 1), while random sites used by roe deer were defined with response 0. The logistic regression indicates thus whether the likelihood of kill sites increase with vegetation density or not, illustrating how the risk of being killed is distributed. Measures of canopy cover, tree basal area, distance

to concealment and proportion of forage were the explanatory variables considered. A data subset for both lynx and hunters were made. For correlated variables in these subsets, the variable yielding the lowest AIC in a single model was chosen for further analysis. StepAIC was used to find the best model, defined as the simplest model with lowest AIC value and $\Delta AIC < 2$. Overdispersion was avoided if the p value was above 0.05, indicating that the explanatory variables fitted the chosen model (Agresti 2002).

Multicollinearity between canopy cover and basal area of spruce, but also between canopy cover and proportion of dead material markedly affected the estimates of the regression coefficients for the hunter model. Unexpected changes due to an approximate linearity between variables is the reason to this phenomenon (Farrar and Glauber 1967). This have been noted to limit biologist to identify ecological relevant patterns that have empirical importance (Graham 2003). Hence, variables that make this problem can be dropped to only get reliable significant coefficients to avoid type II error (Grewal et al. 2004). I dropped out the proportion of dead material for both the lynx and hunter model. Two separate models, including either canopy cover or basal area of spruce as one of the explanatory variables, were made for both lynx and the hunters. This was done due to the assumed importance of these variables to explain risk. Further, proportion of ferns and horsetails was dropped out from the best model for lynx due to the lack of biological causality. A higher biological relevance is then given since unimportant variation is excluded. The models with lowest AIC values ($\Delta AIC < 2$) in synergy with the highest biological relevance gave the final models. Estimates from the models were back-transformed from logit scale to indicate the relative probability of being killed. These models were plotted.

3. Results

3.1 Habitat structure

The Pearson`s correlation coefficient r indicated low correlation between measures of canopy cover, the categories of tree basal area and proportion of forage since the correlation was between ± 0.5 (Zuur et al. 2009). On other hand, correlation was 0.825 between the mean visibility and distance to concealment for a deer. I only included variables with correlation between ± 0.5 in the following analysis to test my predictions (Table 3).

Table 3: Pearson`s correlation coefficient r between numerical variables of habitat characteristics measured at site where roe deer are killed by lynx, randomly observed along GPS trajectories and shot by hunters in southeastern Norway. The matrix was made by using the "polycor" package in R and the "hetcor" function. Variables with correlation coefficients higher and lower than ± 0.5 are in bold (Zuur et al. 2009).

	Habitat characteristics														
Habitat characteristics	Mean canopy cover	Mean basal area of spruce	Mean basal area of pine	Mean basal area of birch	Mean basal area of RAG	Mean basal area of other	Mean visibility	Mean distance to concealment	Proportion dead	Proportion grass	Proportion herbs	Proportion ericaceous species	Proportion ferns & horsetails	Proportion mosses & lichens	Number of RAG stem recruits
Mean canopy cover	1														
Mean basal area of spruce	0.469	1													
Mean basal area of pine	0.127	-0.086	1												
Mean basal area of birch	0.419	0.265	0.003	1											
Mean basal area of RAG	0.300	-0.019	-0.043	0.097	1										
Mean basal area of other	0.398	-0.022	-0.162	0.036	0.120	1									
Mean visibility	-0.267	-0.097	0.008	-0.150	-0.089	-0.064	1								
Mean distance to concealment	-0.250	-0.100	0.001	-0.119	-0.040	-0.076	**0.825**	1							
Proportion dead	0.403	0.265	-0.121	0.287	0.124	0.214	0.152	0.057	1						
Proportion grass	-0.464	-0.284	-0.212	-0.273	-0.133	-0.193	0.156	0.216	-0.451	1					
Proportion herbs	-0.125	-0.182	-0.171	-0.105	0.049	0.077	-0.138	-0.125	-0.239	-0.010	1				
Proportion ericaceous species	0.040	0.004	0.446	0.024	0.037	-0.184	-0.130	-0.094	-0.261	-0.309	-0.306	1			
Proportion ferns & horsetails	0.130	-0.003	-0.175	0.035	0.058	0.116	-0.214	-0.208	-0.101	-0.194	0.014	-0.174	1		
Proportion mosses & lichens	0.090	0.211	0.304	0.039	-0.111	0.026	-0.031	-0.041	-0.200	-0.372	-0.225	0.165	-0.128	1	
Number of RAG stem recruits	0.024	-0.020	-0.003	0.042	0.018	-0.096	-0.173	-0.118	-.0.174	-0.012	0.041	0.164	-0.007	0.062	1

3.2 Vegetation density at kill sites and random roe deer sites

According to chose the simples model if ΔAIC< 2, the best models included only type of sites as the explanatory variable to describe differences in vegetation density between kill sites and random sites used by roe deer. The effect of sex did not enter the model. Canopy cover (%) was higher at lynx kill sites (mean=58.7, 95% CI [48.7, 68.2]) than at random sites used by roe deer (mean=44.9, 95% CI [32.9, 57.3]), and much higher than hunter kill sites (mean=31.4, 95% CI [20.2, HCI=43.7]). The density of spruce (m^2/ha) was much higher at lynx sites (mean=2.37, 95% [1.75, 3.1]) than both random roe deer sites (mean=1.52, 95% CI [0.96, 2.2]) and hunter kill sites (mean=1.56, 95% CI [0.98, 2.32]). These differences in vegetation density are in line with prediction H1.1 and H2.1. On other hand, the basal area of pine (m^2/ha) was high for both lynx (mean=0.60, 95 CI [0.36, 0.89]) and hunter kill sites (mean=0.73, 95 CI [0.40, 1.14]), while low for random roe deer sites (mean=0.25, 95 CI [0.02, 0.53]). The distance to concealment (m) was not consistent with H1.1or H2.1, since no differences were found between the type of sites (table 4, Fig 4).

Table 4: Parameter estimates from the best generalized linear models of vegetation density between sites where roe deer have been killed by lynx, randomly observed along GPS trajectories and shot by hunters in southeastern Norway. Estimates are in mean, standard error (SE) and 95% confidence interval (lower and higher limits). Significant differences are in bold. The estimates are transformed, canopy cover (%) (arcsine-sqrt transformed), basal area of spruce and pine (m^2/ha) and distances to concealment (m) (ln+1 transformed).

		Canopy cover		
Parameter	Mean	SE	Lower	Higher
Intercept	**0.873**	**0.049**	**0.773**	**0.972**
Random roe deer sites vs. lynx kill sites	**-0.138**	**0.062**	**-0.262**	**-0.013**
Hunter kill sites vs. lynx kill sites	**-0.278**	**0.064**	**-0.406**	**-0.149**
		Basal area of spruce		
Parameter	Mean	SE	Lower	Higher
Intercept	**1.215**	**0.100**	**1.015**	**1.445**
Random roe deer sites vs. lynx kill sites	**-0.289**	**0.125**	**-0.540**	**0.038**
Hunter kill sites vs. lynx kill sites	**-0.272**	**0.129**	**-0.531**	**-0.014**
		Basal area of pine		
Parameter	Mean	SE	Lower	Higher
Intercept	**0.474**	**0.082**	**0.310**	**0.638**
Random roe deer sites vs. lynx kill sites	**-0.250**	**0.102**	**-0.455**	**-0.044**
Hunter kill sites vs. lynx kill sites	0.075	0.106	-0.137	0.287
		Distance to concealment		
Parameter	Mean	SE	Lower	Higher
Intercept	3.945	0.082	3.788	4.120
Random roe deer sites vs. lynx kill sites	0.056	0.103	-0.150	0.263
Hunter kill sites vs. lynx kill sites	0.115	0.106	-0.097	0.328

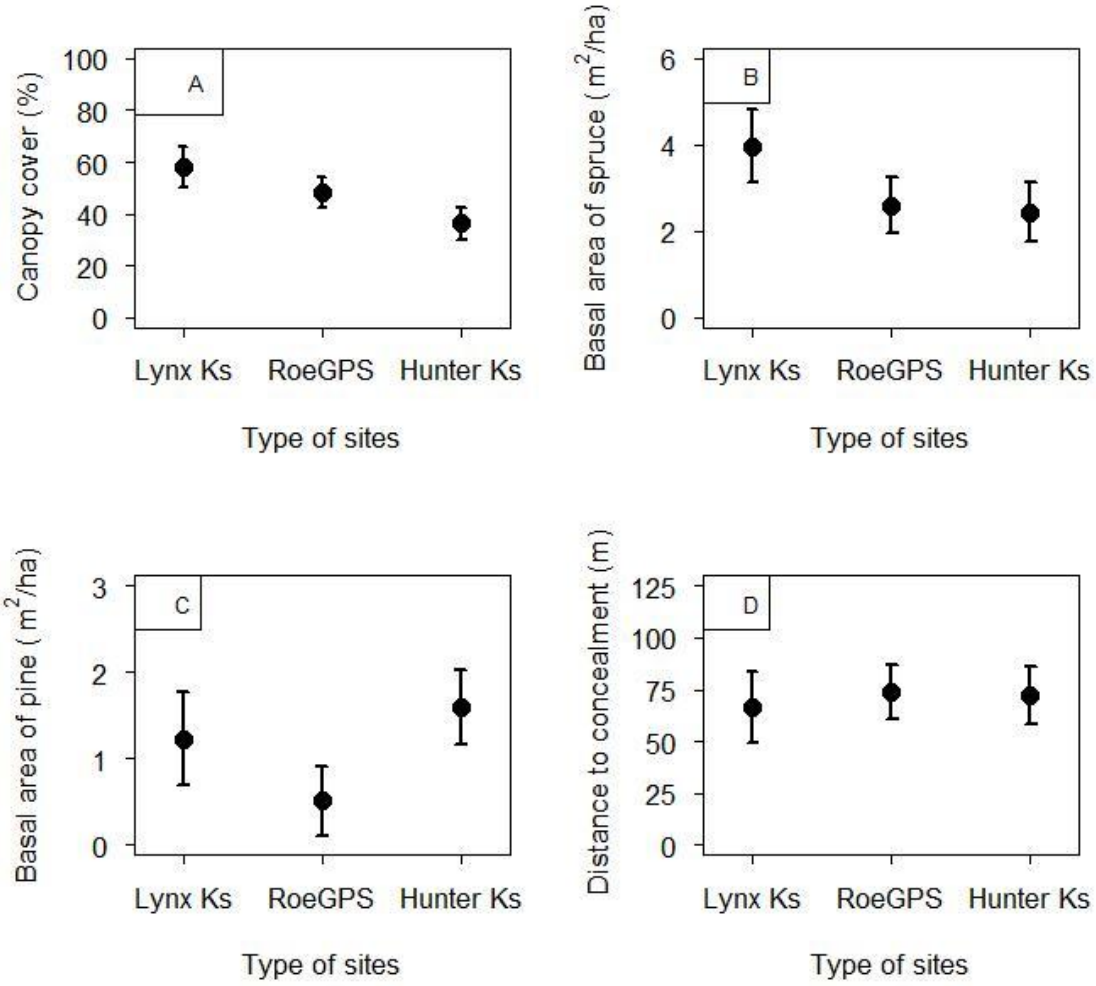

Figure 4: Vegetation density at lynx kill sites (Lynx Ks), random sites used by roe deer (RoeGPS) and hunter kill sites (Hunter Ks) in southeastern Norway. Estimates are in mean and error bars indicate 95% confidence interval. A) canopy cover (%). B) and C) basal area of spruce and pine (m^2/ha). Note that the axes of B) and C) have different scales. D) distance to concealment (m) .

3.3 Individual differences among roe deer and lynx

GLMMs gave no evidence for distinctive individual behavior by roe deer and lynx. The GLMs compared to GLMMs had the lowest AIC-value for both roe deer (AIC 148.6 vs. 154.4) and lynx (AIC 40.8 vs. 46.9).

3.4 Differences in canopy cover in a seasonal aspect

The best model to describe differences in canopy cover at random roe deer sites and lynx kill sites included only season as explanatory variable. Keeping in mind that the vegetation was always measured in the summer, the canopy cover did not differ between seasons where roe deer were killed by lynx and randomly observed (table 5). Not in line with prediction H2.5, roe deer did not use habitats with higher canopy cover during the hunting season.

Table 5: Parameter estimates from the best generalized linear models of canopy cover (%) (arcsine-sqrt transformed) between seasons at random sites used by roe deer and lynx kill sites in southeastern Norway. Estimates are in mean, standard error (SE) and 95% confidence interval (lower and higher limits). Significant differences are in bold.

		Canopy cover at random roe deer sites		
Parameter	Mean	SE	Lower	Higher
Intercept	0.644	0.069	0.504	0.784
Summer vs. hunting season	0.109	0.098	-0.088	0.307
Winter vs. hunting season	0.163	0.098	-0.034	0.362
		Canopy cover at lynx kill sites		
Parameter	Mean	SE	Lower	Higher
Intercept	0.824	0.098	0.628	1.02
Summer vs. hunting season	-0.007	0.136	-0.280	0.265
Winter vs. hunting season	-0.096	0.130	-0.358	0.165

3.5 Forage condition at kill sites and random roe deer sites

The proportion of forage was best described by a model that only included type of sites as explanatory variable, adding sex did not decrease the AIC value more than 2 values. The proportion of grass was lower, while ericaceous species and the number of RAG stem recruits were higher at lynx kill sites compared to the random roe deer sites and hunter kill sites. This finding is partially consistent with prediction H1.2. Sites where roe deer had been shot showed no differences in the proportion of forage compared with sites that were randomly used by roe deer (table 6, Fig 5). This is not in line with prediction H2.2.

Table 6: Parameter estimates from the best generalized linear models of the proportion of grass, herbs and ericaceous species (%) (arcsine-sqrt transformed) and number of RAG stem recruits (ln+ 1 transformed) between sites where roe deer have been killed by lynx, randomly observed along GPS trajectories and shot by hunters in southeastern Norway. Estimates are in mean, standard error (SE) and 95% confidence interval (lower and higher limits). Significant differences are in bold. RAG means rowan, aspen and goat willow.

		Proportion of grass		
Parameter	Mean	SE	Lower	Higher
Intercept	**0.329**	**0.046**	**0.236**	**0.423**
Random roe deer sites vs. lynx kill sites	**0.168**	**0.058**	**0.052**	**0.284**
Hunter kill sites vs. lynx kill sites	**0.137**	**0.059**	**0.017**	**0.257**
		Proportion of herbs		
Parameter	Mean	SE	Lower	Higher
Intercept	0.281	0.032	0.215	0.347
Random roe deer sites vs. lynx kill sites	0.016	0.041	-0.065	0.098
Hunter kill sites vs. lynx kill sites	0.054	0.042	-0.030	0.139
		Proportion of ericaceous species		
Parameter	Mean	SE	Lower	Higher
Intercept	**0.305**	**0.038**	**0.228**	**0.383**
Random roe deer sites vs. lynx kill sites	**-0.171**	**0.048**	**-0.267**	**-0.075**
Hunter kill sites vs. lynx kill sites	**-0.098**	**0.049**	**-0.197**	**0.000**
		Number of RAG stem recruits		
Parameter	Mean	SE	Lower	Higher
Intercept	**1.025**	**0.128**	**0.767**	**1.281**
Random roe deer sites vs. lynx kill sites	**-0.363**	**0.160**	**-0.683**	**-0.043**
Hunter kill sites vs. lynx kill sites	**-0.376**	**0.165**	**-0.706**	**-0.046**

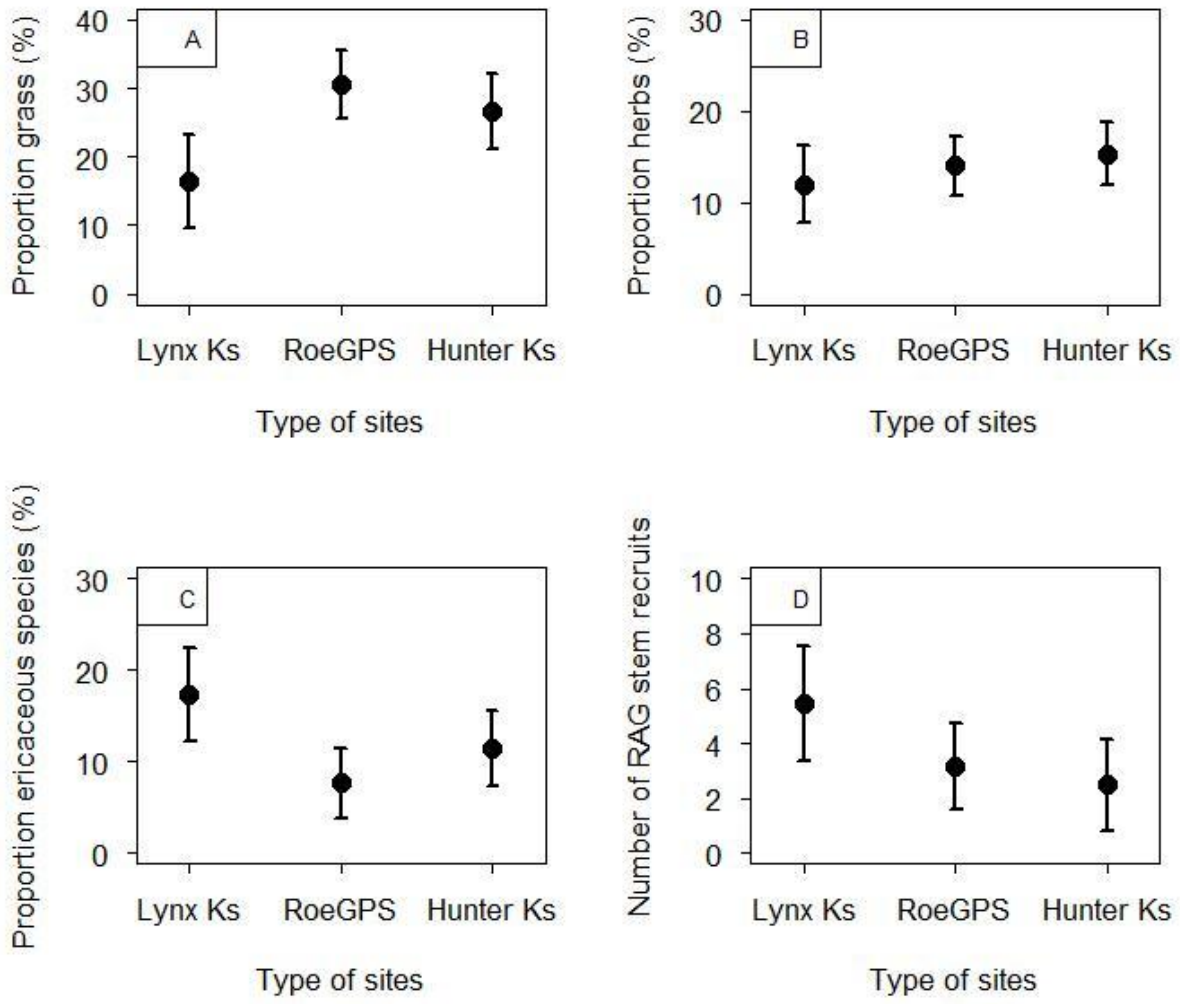

Figure 5: The proportion of potential forage availability between lynx kill sites (Lynx KS), random sites used by roe deer (RoeGPS) and hunter kill sites (Hunter KS) in southeastern Norway. Estimates are in mean and error bars indicate 95% confidence interval. Note different limits for the y- axes. The proportions (%) of A) grass, B) herbs and C) ericaceous species are shown. Figure D) shows the differences in number of stem recruits of RAG (rowan, aspen and goat willow).

3.6 Vegetation density related to weapon types and hunting methods

The AIC value did not decrease more than two values when sex was included as an explanatory variable to describe differences among weapons types and hunting methods. Hence, the best models to describe vegetation density where roe deer were shot included only weapon types and hunting methods as the explanatory variables.

As expected according to prediction H2.3, the vegetation density differed between sites where hunters had used different weapon types. Canopy cover (%) was higher at sites where hunters had used shotgun (mean=51.1, 95% CI [33.8, 68.2]) than at sites where hunters had used rifle (mean=25.30, 95% CI [18.06, 33.3]). In addition, sites where hunters had shot roe deer with shotgun had higher basal area of spruce (m^2/ha) (mean=2.9, 95% CI [1.74, 4.56]) than sites where roe deer had been shot with a rifle (mean=1.21, 95% CI [0.85, 1.63]). On the other hand, neither basal area of pine (m^2/ha) or distance to concealment (m) showed any differences (table 7, Fig 6).

Sites where hunters had used different hunting methods had also different vegetation density, providing support for prediction H2.4. Canopy cover (%) was higher where roe deer had been shot by a stalking hunter (mean=53.8, 95% CI [33.4, 73.7]) than shot by a hunter that were drive hunting (mean=32.0, 95% CI [23.7, 40.8]). In contrast, no differences in canopy cover existed between drive hunting and hunters that used the "sit and wait" method (mean=18.1, 95% CI [6.6, 33.7]). Basal area of spruce (m^2/ha) showed no differences between hunting methods (table 8, Fig 6). On other hand, basal area of pine was higher where roe deer were shot by stalking hunters (mean=1.92, 95% CI [0.85, 3.62]) compared to drive hunting (mean=0.72, 95% CI [0.40, 1.10]) and "sit and wait" hunting (mean=0.33, 95% CI [-0.10, 0.97]). Distance to concealment (m) differed between waiting hunters (mean=70.80, 95% CI [51.56, 97.10]) and drive hunting (mean=49.85, 95% CI [42.33, 58.74]), which indicates that waiting hunters had greater overview. Stalking hunters (mean=66.1, 95% CI [45.76, 95.45]) had not better overview then hunters that used drive hunting.

Table 7: Parameter estimates from the best generalized linear models of vegetation density between sites where roe deer have been shot by different weapon types in southeastern Norway. Estimates are in mean, standard error (SE) and 95% confidence interval (lower and higher limits). Significant differences are in bold. The estimates are transformed, canopy cover (%) (arcsine-sqrt transformed), basal area of spruce and pine (m^2/ha) and distances to concealment (m) (ln+1 transformed).

		Canopy cover		
Parameter	Mean	SE	Lower	Higher
Intercept	**0.527**	**0.044**	**0.439**	**0.615**
Shotgun vs. rifle	**0.269**	**0.088**	**0.092**	**0.446**
		Basal area of spruce		
Parameter	Mean	SE	Lower	Higher
Intercept	**0.793**	**0.088**	**0.617**	**0.969**
Shotgun vs. rifle	**0.569**	**0.177**	**0.092**	**0.924**
		Basal area of pine		
Parameter	Mean	SE	Lower	Higher
Intercept	0.488	0.099	0.290	0.686
Shotgun vs. rifle	0.144	0.199	-0.254	0.542
		Distance to concealment		
Parameter	Mean	SE	Lower	Higher
Intercept	4.049	0.080	3.889	4.210
Shotgun vs. rifle	-0.018	0.160	-0.338	0.301

Table 8: Parameter estimates from the best generalized linear models of vegetation density between sites where roe deer are shot by using different hunting methods in southeastern Norway. Estimates are in mean, standard error (SE) and 95% confidence interval (lower and higher limits). Significant differences are in bold. The estimates are transformed, canopy cover (%) (arcsine-sqrt transformed), basal area of spruce and pine (m^2/ha) and distances to concealment (ln+1 transformed).

		Canopy cover		
Parameter	Mean	SE	Lower	Higher
Intercept	**0.601**	**0.046**	**0.509**	**0.693**
Sit and wait vs. drive hunting	- 0.161	0.090	-0.341	0.018
Stalking vs. drive hunting	**0.223**	**0.104**	**0.014**	**0.432**
		Basal area of spruce		
Parameter	Mean	SE	Lower	Higher
Intercept	0.963	0.096	0.771	1.156
Sit and wait vs. drive hunting	-0.188	0.188	-0.565	0.188
Stalking vs. drive hunting	0.152	0.218	-0.284	0.589
		Basal area of pine		
Parameter	Mean	SE	Lower	Higher
Intercept	**0.542**	**0.101**	**0.340**	**0.744**
Sit and wait vs. drive hunting	-0.255	0.197	-0.649	0.139
Stalking vs. drive hunting	**0.531**	**0.229**	**0.073**	**0.989**
		Distance to concealment		
Parameter	Mean	SE	Lower	Higher
Intercept	**3.929**	**0.080**	**3.769**	**4.089**
Sit and wait vs. drive hunting	**0.345**	**0.156**	**0.032**	**0.659**
Stalking vs. drive hunting	0.278	0.181	-0.084	0.642

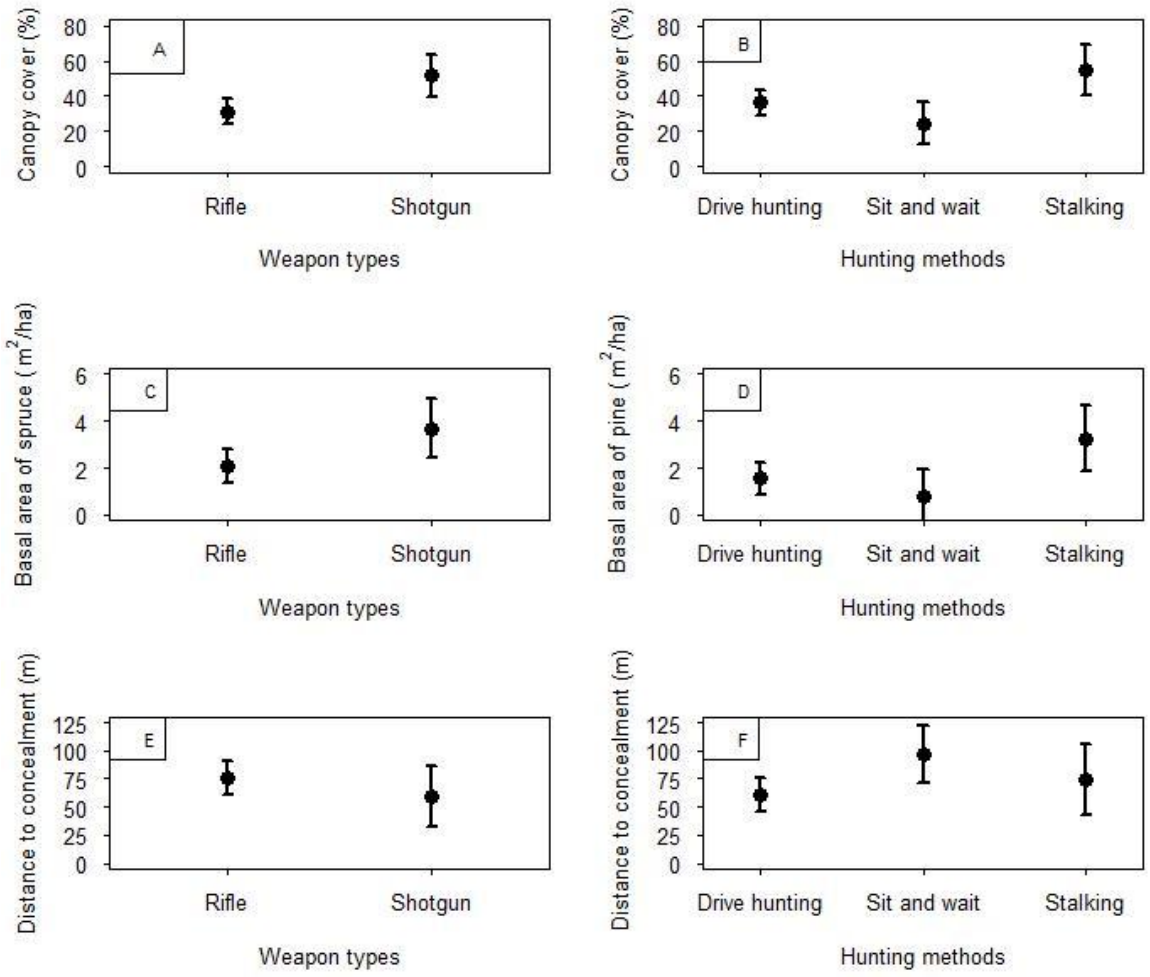

Figure 6: Vegetation density at hunter kill sites where roe deer are shot by different weapon types and use of different hunting methods in southeastern Norway. Estimates are in mean and error bars indicate 95% confidence interval. A) and B) canopy cover (%). C) and D) illustrating differences in the basal area of spruce and pine (m^2/ha). The distance to concealment (m) for a deer is shown in E) and F).

3.7 Contrasting predation risk

The best logistic regression model indicated that the relative probability of being killed by lynx was best described by the basal area of spruce, number of RAG stem recruits and the proportion of grass and herbs. The hunter model included canopy cover, basal area of spruce and pine and the proportion of grass and ericaceous species. For lynx and hunters, al other models had a higher AIC value, △ AIC < 2, and included variables without biological relevance. Four models are visualized due to multicollinearity between canopy cover and basal area of spruce. As predicted in H1.1 and H2.1, roe deer face higher risk of lynx predation in habitat with dense vegetation, while risk of being shot by hunters is related to habitats with low vegetation density. The relative probability of being killed by lynx increased most along a gradient with increasing basal area of spruce. Increasing canopy cover did also increase the relative probability of being killed by lynx but in a lower degree. The hunters showed an opposite pattern. The relative probability of being killed by hunters increased most with decreasing canopy cover, and less for basal area of spruce. These models show a contrasting risk pattern of being killed by lynx and hunters (Fig 7).

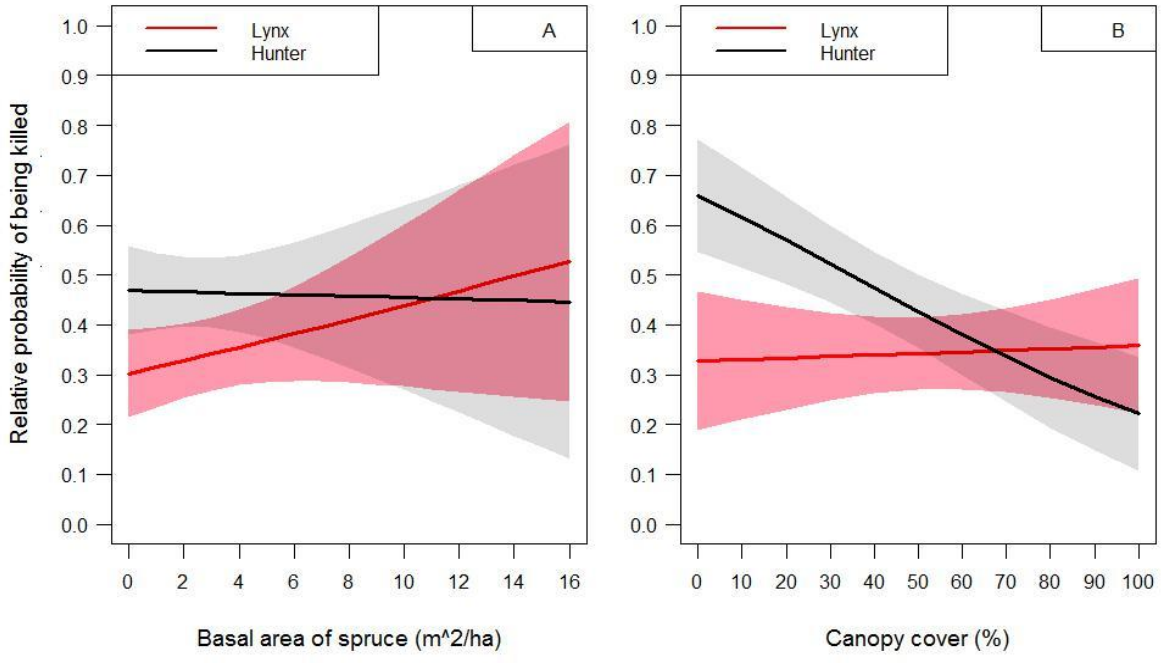

Figure 7: In southeastern Norway, roe deer face contrasting risk of being killed by lynx and hunters with increasing basal area of spruce (m^2 /ha) and canopy cover (%). The risk of lynx predation increases with higher basal area of spruce and canopy cover: The risk of being shot by hunters increase with decreasing basal area of spruce and canopy cover. The relative probability of being killed is used as a measure of risk, given as the likelihood of kill sites to increase with vegetation density or not. The figures represent the best logistic regression models according to the principle of parsimony given as the simplest outcome with lowest AIC, △ AIC < 2 and highest biological relevance.

4. Discussion

How habitat use by ungulates is influenced by the risk of being killed by natural predators and hunters has become topical in light of the re-colonization of apex predators and extensive human harvesting (Laundre et al. 2001, Ciuti et al. 2012, Cromsigt et al. 2013). Multi-predator studies seeking knowledge to understand how predation risk can structure prey in space (Atwood et al. 2009). In such a multi-predator setting in a boreal forest ecosystem, I found that the risk of being killed for roe deer was indeed related to specific habitat characteristics. In line with the hypotheses H1 and H2, dense habitat increased risk of lynx predation, while open habitats in general increased the risk of being shot by hunters. Habitat use by roe deer was squeezed between habitats in risk of being killed by these predators with contrasting hunting style. This suggests it may be difficult for roe deer to avoid predation risk from both lynx and hunters at the same time by using one single spatial anti-predator behavior.

4.1 The lynx – the killer in the bushes

Several studies have indicated that the lynx is an ambush predator, hunting in dense habitats with great heterogeneity in visibility (Murray et al. 1995, Nilsen et al. 2009, Belotti et al. 2013). My findings underpin this view. As predicted in H1.1, in habitats with high canopy cover and great basal area of spruce, roe deer are highly at risk of being killed by lynx.

Encounter rate and hunting success are found to be two important factors for explaining spatial patterns of predation risk (Hebblewhite et al. 2005). How roe deer face the risk of being killed by lynx can be related to these two components. It is documented that the lynx inhabits suitable roe deer habitats (Odden et al. 2008). Lynx that encounter roe deer in dense habitat may have greater hunting success due to better stalking conditions. The lynx is seldom successful when an attack is initiated at longer distance than 50 m (Haglund 1966). Dense habitats are likely to give the lynx higher opportunity to attack from a shorter distance and initiate ambush attacks. Reduced opportunity to detect the lynx in dense habitats is likely to make roe deer more at risk in dense habitats compared with open habitats. In line with this, dense habitat may make it harder to maneuver for a deer, then making it easier for the lynx to catch it (Mysterud and Østbye 1999).

On other hand, not in line with prediction H1.1, concealment measured as reduced visibility *per se* was not related to higher lynx predation risk for roe deer. Habitats with high heterogeneity in visibility may enable the predator to remain hidden, but in same time follow how prey are moving (Belotti et al. 2013). No differences in visibility between sites where roe deer allocate most time compared to lynx kill sites may imply that overall visibility is not the

main factor that influence the hunting success for the lynx. Perhaps, the lynx can use the terrain from certain directions to remain undiscovered, making the horizontal vegetation cover unimportant for the hunting success. Note that this is speculations, and it is not possible to fully separate these possibilities based on the current study.

4.2 The hunter – the ultimate predator that kills everywhere

My study highlights that the risk of being killed by hunters might not always be as spatially predictable as suggested in Cromsigt et al. (2013). Hunters choose hunting methods and use weapon types adaptively to increase the encounter rate and hunting success (Andersen et al. 2004). Several hunting methods in combination with different weapon types indicate that hunters are extremely flexible and may impose risk in all types of habitats. The different hunting methods induce a certain level of risk all across the environmental range of habitat characteristics. Confirming prediction H2.4, the "sit and wait" method imposes the greatest risk in open habitats, drive hunting in middle dense habitats, while stalking in the densest habitats. Hunters are in general thought to impose risk in open habitats due to use of rifles (Ciuti et al. 2012, Lone et al. 2014) but my findings indicate that hunting risk cannot be categorized that simply.

The risk pattern among hunting methods can probably be linked to properties of the weapons used and the weapon restrictions given for different parts of the hunting season. Rifles are the only legal weapon in the early part of the season when the "sit and wait" and stalking method are normally used. Vegetation density where roe deer were killed by hunters using rifle matches "sit and wait" hunting, but not stalking, since roe deer were shot by rifle hunters in open habitats. This is in line with prediction H2.3. Hunters normally use rifles with scopes to hit targets that are standing still with one single shot and one heavy projectile on long distances with high accuracy. Hence, open habitats are likely to increase the risk of being shot by rifle since the vegetation density increase the ability to detect a deer and initiate a clean shot. Interestingly, canopy cover and basal area of pine were quite high at this kill sites where hunters had been stalking roe deer. Several hunter kill sites were located in the valleys with open pine forest with heather. Rifle shots are then still possible, and the hunter may be concealed during the stalking much in the same way as lynx, making hunting greatly successful in this type of habitat.

In addition, roe deer that seek into dense canopy cover were more at risk of being shot by hunters that are using shotgun, as pointed in prediction H2.3.

In fact, the basal area of spruce was higher where roe deer were shot by shotgun (2.9 m^2/ha) than killed by lynx (2.37 m^2/ha). This type of weapon has low accuracy, but with hundreds of small bullets being fired, it is designed to hit targets in motion on short distances. It is therefore common to use especially during drive hunting with dogs. However, the vegetation density at kill sites from drive hunting and shotgun are not fully matched, most likely since rifles are also common to use during drive hunting then with hunters situated in more open habitats.

Since roe deer hunters in my study area were spatially unpredictable, an optimal strategy for avoidance of humans by roe deer is less obvious. Indeed, contrasting to prediction H2.5, I found no evidence for that roe deer moved into denser habitats during the hunting season as might be expected if risk was always higher in open habitat during the hunting season. This result was based on only five individuals, but use of mixed models showed no evidence of any individual differences, suggesting it is likely that the habitat characteristics represented by these five individuals were representative. Thus, this study is in contrast to Benhaiem et al. (2008) that found evidence for reduced selection of patches with high forage quality by roe deer where the risk of being shot was high. On other hand, the study by Benhaiem and colleagues was conducted in France with a different hunting culture, suggesting behavioral responses to hunting may vary across Europe's many different hunting cultures.

4.3 The use of safe and risky habitats by roe deer

The presence of a predator may influence how resources are exploited and how the physical landscape is used (Brown 1988). According to cover, roe deer allocate more time in habitats without risk of being killed by lynx. As pointed in hypothesis H1, roe deer may face a tradeoff between availability to cover and lynx predation. On other hand, the lynx kill sites show that roe deer also have used dense habitats. The question why roe deer move into denser habitats though the risk of being killed is higher is thus interesting. The main dilemma for prey are trying to select habitats that satisfy the requirements of resources but at the same time are safe (Laundre 2010). However, safe habitats provide not always the availability of resources that are necessary to maintain fitness enhancing activities (Hernandez and Laundre 2005). Others have argued that roe deer use dense habitats since it reduces the exposure to predators as well as energetically cost due to locomotion in snow on searching for food and heat loss (Mysterud and Østbye 1995, Mysterud and Østbye 1999, Ratikainen et al. 2007). The indirect costs of avoiding dense habitats with high risk of lynx could be too high for it to be worth it for roe

deer. Hence, at least during harsh winters, roe deer may freeze and starve to death if dense habitats are avoided due to its low fat reserves and high metabolic rate (Holand 1990, Holand et al. 1998). Thus, I suggest that necessity to get enough food in synergy with climatic factors and predation risk in open habitats determine how roe deer use habitats that make it in risk of lynx predation.

Roe deer allocate also less time in open habitat where the risk of being shot is higher. Though prediction H2.2 indicates that hunters should have shot roe deer where the availability of forage was high, this was not the case. This is counterintuitive considering that open habitats should have better growth conditions for high quality plants like herbs. Neither did I find any differences in the quantity of herbs at lynx kill sites compared to random roe deer sites. On other hand, lynx kill sites relative to random roe deer sites had a lower availability of grass but higher availability of ericaceous species and RAG stem recruits. The forage availability at lynx kill sites is thus only partially consistent with prediction H2.2. One important thing to note is that the sampling of forage was done at a fine scale. Disturbance in the data is then likely. For instance, the hunters might have shot the roe deer when it was traveling to its feeding site or chased by a dog. In same case, the lynx might have chased the deer a short distance or dragged it in a random direction. I will thus not make any clear suggestions about whether roe deer are trading off the availability of forage against reduced predation risk, but my findings may indicate that roe deer not sacrifice good availability of forage against reduced predation risk. This type of suggestions is not a concern for the vegetation density measurements like canopy cover and tree basal area since these measurements were registered on a coarser scale. Hence, suggestions on whether the predation risk related to dense and open habitat can structure roe deer in the physical landscape are still possible.

4.4 Habitat use by roe deer in a multi-predator squeeze

How prey respond to the distribution of predation risk in the physical landscape, open vs. dense habitats, is determined by what behavior that enhances the fitness most (Lima and Dill 1990, Laundre 2010). My study indicates that roe deer face contrasting predation risk from lynx and hunters (see also Lone et al. 2014), but with considerable variation due to the flexibility in the hunters. Habitat use by roe deer is squeezed in the middle of habitats with risk of being killed by these predators. A selective habitat use that reduces predation risk by lynx might thus increase the risk of being shot and vice versa. In a similar way, elk that move into denser habitats to avoid wolf predation are at higher risk of being killed by cougars

(*Puma concolor*) (Atwood et al. 2009). In addition, hunters that shoot elk in open areas are selecting for individuals that expose themselves more to cougar predation (Ciuti et al. 2012). Contrasting predation risk by multiple predators might then suppress a spatial anti-predator response due to a net higher predation rate if changes are made (Cresswell and Quinn 2013). The "landscape of fear" will by this multi-predator squeeze become flatter since risky peaks and safe valley bottoms are less distinctive, making an adaptive anti-predator response harder to sort out. A spatial anti-predator response by roe deer in this risk landscape is then less likely since the gain compared with the cost might not improve the fitness at al. Hence, as indicated by Gervasi et al. (2013), human activities in synergy with predation by a large carnivore seem to limit behavioral changes in roe deer.

On the other hand, a spatial anti-predator response might be more advantageous when predation risk patterns align, as there is a potential increase in survival relative to both predators. Roe deer face "double risk" from lynx and human predation in habitats with high terrain ruggedness (Lone et al. 2014). Habitats with high basal area of pine could also be a "double risk" habitat given my findings. The possibility of clean shots but also good stalking conditions for the lynx seems to make up high peak in the risk landscape. The potential gain by avoiding this habitat is thus likely high if it not make to high indirect effects.

Though a chronic shift in habitat use by roe deer is less likely when predation risk is contrasting, it does not mean that roe deer cannot respond to risk in one or another way. Anecdotal evidence show that roe deer acutely use more open habitats when a lynx initiates an attack (Mysterud et al. 1998). Acute use of dense habitats is also suggested to be the best response to humans by roe deer (Bonnot et al. 2013, Sonnichsen et al. 2013). This type of dynamic habitat selection is supposed to be the most adaptive predator avoidance strategy to enhance the fitness when predation risk is fluctuating (Latombe et al. 2014). In line with this, the lynx predation is fluctuating in space and time due to that the lynx have large home ranges (Sunde et al. 2000, Linnell et al. 2001, Andersen et al. 2005, Herfindal et al. 2005). Human predation is also fluctuating in space and time since hunters are not active 24 hours during one day or every day during the hunting season. Hence, a temporal separated selection of habitats between roe deer, lynx and hunters may safeguard the resource availability for roe deer though resources and predation risk peak in the same habitat. A strict spatiotemporal separation could then be a reason why roe deer lack an alteration in habitat selection when the lynx have re-colonized and the risk of being shot is present (Ratikainen et al. 2007, Samelius et al. 2013, Lone et al . 2014). However, whether or not a dynamic habitat selection is the most adaptive anti-predator response by roe deer cannot be suggested by this study due to lack

of this type of data.

Another important predator on roe deer is the red fox (*Vulpes vulpes*) (Jarnemo and Liberg 2005), for which no data was available. Red fox mainly targets newborns (Panzacchi et al. 2008) but also adult roe deer face some predation risk if the snow is very deep (Cederlund and Lindstrom 1983). Roe deer populations with high density are found to face higher risk of red fox predation than lynx predation (Melis et al. 2013). Higher predation risk by the red fox in absence of the lynx due to a mesopredator release might be a plausible explanation (Helldin et al. 2006, Elmhagen et al. 2010, Ritchie et al. 2012). In the future, mesopredators as common as the red fox should be included in multi-predator studies to understand whether or not prey can be structured in space by this type of predator.

5. Conclusion

This study of roe deer habitat use reminds us that the distribution of prey is influenced by the risk of being killed by multiple predators. Multiple predators with unlike hunting styles have different hunting efficiency among habitat characteristics that influence the overall formation of risky peaks and safe valleys in the "landscape of fear". The lynx are hiding in the bushes with high canopy cover and great basal area of spruce, making this habitat risky for roe deer. Despite the risk of being shot is in general related to open habitats, this study indicates that hunting risk cannot be categorized that simply. The combination of hunting methods and weapon types make the distribution of risk imposed by hunters hard to predict in the physical landscape. One plausible reason why roe deer not select denser habitat during the hunting seasons in southeastern Norway is then likely to be due to the unpredictability of the hunters. The contrasting risk of lynx and hunters make a relatively flat overall risk landscape where it is difficult for roe deer to sort out one single spatial anti-predator response that reduce the predation risk from both predators. A heterogeneous distribution between roe deer and these two main predators given cover indicates that roe deer concentrate most of its time in safe habitats. On other hand, roe deer may not sacrifice good forage against reduced predation risk. The behavior of roe deer seems to be to avoid starvation and face the direct lethal effect of predation.

I suggest that further studies should focus on how habitat use by prey is related to the temporal variation of risk by multiple predators. This type of study can illustrate whether the habitat use are adaptive in a more coherent setting, giving higher understanding of the direct and indirect effects of predation.

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